

**DIRECT AND INDIRECT EFFECTS OF ENVIRONMENTAL  
VARIABILITY ON GROWTH AND SURVIVORSHIP OF  
PRE-REPRODUCTIVE JOSHUA TREES, *YUCCA BREVIFOLIA*  
ENGELM. (AGAVACEAE)<sup>1</sup>**

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- **Premise of study:** Accurate demographic information about long-lived plant species is important for understanding responses to large-scale disturbances, including climate change. It is challenging to obtain these data from desert perennial plants because seedling establishment is exceptionally rare, and estimates of survival are lacking for their vulnerable early stages. Desert wildfires, urbanization, and climate change influence the persistence of the long-lived *Yucca brevifolia*. Quantitative demographic attributes are crucial for understanding how populations will respond to disturbances and where populations will recede or advance under future climate scenarios.
- **Methods:** We measured survival in a cohort of 53 pre-reproductive *Y. brevifolia* at Yucca Flat, Nevada, USA, for 22 yr and recorded their growth, nurse-plant relationships, and herbivory.
- **Key results:** Herbivory by black-tailed jackrabbits (*Lepus californicus*) caused severe losses of plants during the first and second years (45% and 31%, respectively). Surviving plants experienced <2.5% annual mortality. Survival for the population was 19% over 22 yr. Plants <25 cm in height had lower life expectancy. Average growth rate ( $\pm$  SD) for plants that survived to the last census was  $3.12 \pm 1.96$  cm yr<sup>-1</sup>, and growth rates were positively associated with precipitation. Thirty-year-old *Y. brevifolia* had not yet reproduced.
- **Conclusions:** A rare establishment event for *Y. brevifolia* during 1983–1984, triggered by above-average summer rainfall, provided a unique opportunity to track early survival and growth. Infrequent but acute episodes of herbivory during drought influenced demography for decades. Variability in survival among young *Y. brevifolia* indicates that size-dependent demographic variables will improve forecasts for this long-lived desert species under predicted regional climate change.

**Key words:** Demography; drought; El Niño Southern Oscillation; herbivory; Joshua tree; life history; Mojave Desert; nurse plants; pre-reproductive.

Quantitative demographic data are essential for predicting future impacts of land use and climate change on the migration and persistence of long-lived plant species (Harper, 1977; Menges, 2000). *Yucca brevifolia* Engelm. (Joshua tree, Agavaceae)—an arborescent succulent species of the Mojave Desert (Benson and Darrow, 1981)—has endured for millenia, but rapid changes in regional climate have recently raised concern

about its long-term survival. Species habitat models based on contemporary and projected climates suggest that *Y. brevifolia* will lose habitat in the southern part of its current range, which will partly be offset by new potential habitat to the north (Cole et al., 2011; Smith et al., 2011; Barrows and Murphy-Mariscal, 2012). However, bioclimatic habitat models alone do not integrate the complex interactions between life history, disturbance regimes, and distribution patterns that are critical for determining extinction risks under future climate change scenarios (Keith et al., 2008). For example, recruitment of *Y. brevifolia* requires a convergence of events, including fertilization by unique pollinators (Pellmyr and Segraves, 2003), seed dispersal and caching by rodents (Vander Wall et al., 2006; Waitman et al., 2012), and seedling emergence from a transient seed bank triggered by isolated late-summer rainfall (Reynolds et al., 2012). Alignment of these convergent events likely results in successful establishment of new seedlings only a few times in a century (Wallace and Romney, 1972). In addition, individual *Y. brevifolia* that are <1 m tall are more vulnerable than large size classes to wildfires, herbivory, and periodic drought (DeFalco et al., 2010). Thus, distribution models for this species that ignore variable age- or size-class responses may poorly predict the suitability of habitat under changing climate and land-use scenarios.

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Many demographic variables are known for the adult life stages of *Y. brevifolia*. Pollination success and reproductive mutualists (Yoder et al., 2013), seed dispersal modes and distances (Vander Wall et al., 2006; Waitman et al., 2012), and adult growth rates (summarized in Rowlands, 1978; Comanor and Clark, 2000; Gilliland et al., 2006) have been previously estimated for *Y. brevifolia*. Even the ecotypes of *Y. brevifolia* (i.e., *Y. b. brevifolia* and *Y. b. jaegeriana*) are pollinated by different symbiotic moth species (*Tegeticula synthetica* and *T. antithetica*, respectively) (Rowlands, 1978; Pellmyr and Segraves, 2003). Despite detailed information about adult life stages, estimates for survival on pre-reproductive *Y. brevifolia*—likely the most dynamic size class for modeling demographic changes to expected climate variability—are currently unknown.

As part of the Basic Environmental Compliance and Monitoring Program (BECAMP) at the Department of Energy, Nevada National Security Site (NNSS; formerly “Nevada Test Site”), the growth and survivorship of pre-reproductive *Y. brevifolia* were measured from 1989 through 1994 (Hunter, 1995). Here, we report the results of the entire monitoring survey, including subsequent years when we remeasured the sample population to establish growth and survivorship rates of *Y. brevifolia* at a single site in relation to size, climate, and nurse-plant associations. These size-specific vital rates will provide valuable information for future demographic and climatic models of *Y. brevifolia* populations, which need to account for the differential influences of abiotic and biotic factors on demographic life stages of the species.

We hypothesized that pre-reproductive *Y. brevifolia* that rapidly attain a large size have a survivorship advantage over those with slower growth. We also hypothesized that seasonal precipitation and nurse-plant association regulate plant growth and seedling survival, respectively. Ultimately, by understanding these influences on *Y. brevifolia*—particularly for the vulnerable pre-reproductive age/size classes that are the focus of this study—we expect that future demographic modeling for *Y. brevifolia* populations will be improved for different parts of its range and under different climate scenarios.

## MATERIALS AND METHODS

**Study area**—The study area is on the west side of Yucca Flat (UTM 102455 E–583750 N, projection WGS 84) within the NNSS in Nye County, Nevada, at 1245 m elevation a.s.l. The vegetation assemblage is a Mojave Desert shrubland composed primarily of *Lycium andersoni* (boxthorn) and *Grayia spinosa* (spiny hop-sage) in association with *Ephedra nevadensis* (Mormon tea), *Atriplex canescens* (saltbush), *Krascheninnikovia lanata* (winterfat), and widely scattered *Y. brevifolia* that are visually prominent on the landscape (Beatley, 1975; Willis and Ostler, 2001; Webb et al., 2003). While the hybrid zone between *Y. brevifolia brevifolia* and *Y. b. jaegeriana* is <80 km in a straight-line distance from this study area (Smith et al., 2009), the dominant ecotype at this location is *Y. b. brevifolia* (hereafter referred to as *Y. brevifolia*). Soils are deep, mixed-source alluvium derived from granite, rhyolite, and volcanic tuff. Climatic data for the full period of record were obtained from the Buster Jangle “Y” station (BJY), located 6 km northwest of our study area at 1237 m a.s.l. and with a 51-yr (1960–2011) average precipitation of  $161.6 \pm 77.4$  mm (NOAA, 2011; Fig. 1). Twenty-year average (1981–2001) December minimum and July maximum air temperatures are  $-3.2^\circ\text{C}$  and  $35.2^\circ\text{C}$ , respectively (Department of Energy, 2013).

**Cohort establishment and plant measurements**—Growth, survivorship, potential nurse-plant associations, and herbivore activity were measured for a cohort of pre-reproductive *Y. brevifolia* initially measured during May 1989. These plants were sampled annually from 1989 to 1994 (Hunter, 1995) and again in 2005, 2008, 2009, and 2011. The pre-reproductive population was initially observed during a mark-recapture survey of *Uta stansburiana* (side-blotched lizard) on a 1.1-ha plot, when close inspection of dense shrub canopies revealed small *Y. brevifolia* plants sheltered beneath them. The locations of 53 plants were initially recorded during those surveys. Subsequently, each small plant was relocated, using a permanent grid in combination with small aluminum stakes inscribed with a unique number and placed near the base of each plant (Hunter, 1995). These seedlings are not to be confused with root sprouts, because only 2 adult *Y. brevifolia* occur on the entire plot, and seedlings occurred beyond 6 m of either adult.

We measured height and condition of the plants (e.g., signs of herbivory or other disturbance) on each visit. Although others have documented negative growth, or shrinkage of *Y. brevifolia* (Gilliland et al., 2006), we assumed that many of the differences were due to variation in surface roughness, litter accretion, soil erosion or accumulation, and/or herbivory. Thus, only zero or positive measurements were included in growth-rate calculations. The plants were considered alive if leaves were green, indicating chlorophyll. We noted where *Y. brevifolia* were growing among the shrub interspaces (i.e., outside the drip line, which is the outermost perimeter of the canopy from which precipitation would drop vertically to the soil surface), within the canopy but touching the drip line, or completely inside the shrub canopy. Species of shrub cover were recorded with

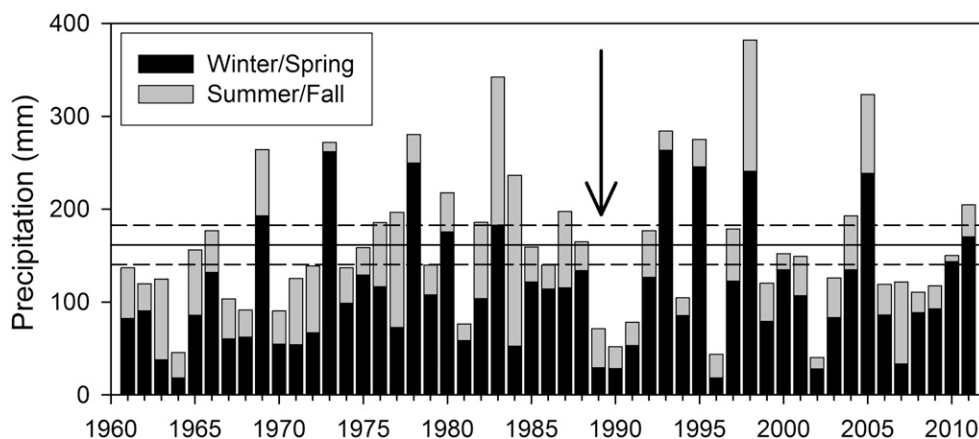


Fig. 1. Precipitation for the hydrological year (October–September) during the expected establishment and growth period for a cohort of 53 *Yucca brevifolia* at the Nevada National Security Site, southern Nevada, USA. Seasons are denoted as winter/spring (October–May) and summer/fall (June–September). Monthly data are from the Buster Jangle “Y” station (NOAA, 2011). Solid and dashed horizontal lines are the mean and 95% confidence interval, respectively. Vertical arrow denotes first census of pre-reproductive *Y. brevifolia*.

notes on individuals or aggregates of plants. Cause of mortality was determined in the field. Signs of herbivory, such as chewed leaves, stems, or roots, were noted and identified using the conspicuous evidence of tooth marks and the accumulation of fecal pellets left by *Lepus californicus* (black-tailed jackrabbit).

**Statistical analyses**—We related precipitation and mean change in height between census periods using linear regression. We calculated a survivorship function and curve based on the yearly mortality rates for the *Y. brevifolia* cohort, using the Kaplan-Meier estimator (Kaplan and Meier, 1958). Despite the long break in sampling from 1994 to 2005, the occurrence of only two deaths during this period allowed us to estimate a survival curve with reasonable accuracy. The survival time of pre-reproductive *Y. brevifolia* in relation to initial height and nurse-plant association (within canopy vs. canopy edge) were analyzed using  $\chi^2$  analyses. In addition, to investigate the effects of initial plant height and nurse-plant location on survivorship during the study period, we fit survival-regression models using the Weibull distribution. All analyses used the core “survival” package in R (functions “survfit” and “survreg”; Therneau and Lumley, 2009; R Development Core Team, 2012).

## RESULTS

**Precipitation**—Exceptionally high summer precipitation (July–September) fell in 1983 and 1984 (172 and 184 mm, respectively). These heavy-rain events were likely responsible for the emergence of *Y. brevifolia* seedlings (Reynolds et al., 2012) that we censused in 1989 as 5- to 6-yr-old plants. Compared with other precensus years with above-average precipitation (e.g., 1973, 1976–1978, 1980), only one other year within the previous two decades had close to the high summer–fall precipitation of the mid-1980s (1977: 124 mm). Severe drought conditions prevailed during the first few years of census (44%, 32%, and 48% of 51-yr average in 1989, 1990, and 1991, respectively). Precipitation fell mostly in December–March and was above average in 1992 and 1993 (Fig. 1; NCDC, 2012), alleviating the prior severe drought conditions. In the years between the initial annual measurements and resumption of measurements in 2004, precipitation fluctuated widely, varying from the record high of 374 mm in 1998 to the record low of 38 mm in 2002. Rainfall was well above average in 2004, 2005, and 2010 (265, 233, and 250 mm, respectively), but most years in the first decade of the 21st century had below-average precipitation.

**Mortality and survival of pre-reproductive *Y. brevifolia***—Between May 1989 and March 1990, 45% (24 of 53) of the *Y. brevifolia* were killed by *L. californicus* when precipitation was low, and by the end of August 1990, an additional 9 plants were consumed (total mortality = 62%). After the initial losses, we found that annualized population mortality was generally low, at 2.5% yr<sup>-1</sup> (Fig. 2). We made only one observation of a marked plant that died solely as a result of drought, as evidenced by the presence of the essentially undisturbed, yet desiccated, plant.

After 22 yr, 10 individuals (18.9%) of the original cohort of 53 nonreproductive *Y. brevifolia* were still living. The height of *Y. brevifolia* at the start of the study in 1989 was a significant predictor of survival time ( $\chi^2 = 40.65$ ,  $P < 0.0001$ ). Six of the seven tallest plants measured in 1989 were among those still alive in 2011, comprising 86% of the surviving cohort. Predicted survival times derived from the regression model indicate that pre-reproductive *Y. brevifolia* with heights  $\geq 25$  cm have a much longer life expectancy, as indicated by the inflection point in the regression curve (Fig. 3A). Pre-reproductive *Y. brevifolia* with initial heights  $\geq 25$  cm had an overall survival

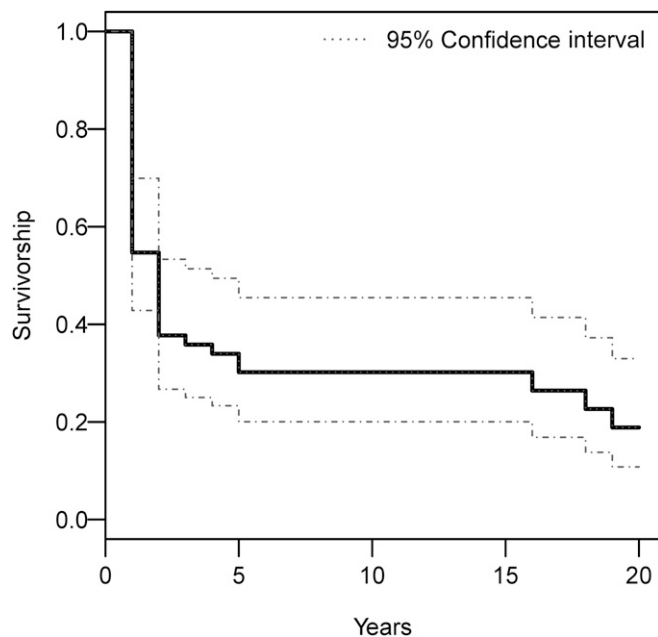


Fig. 2. Survivorship curve for 53 *Yucca brevifolia* that were monitored for 22 yr at Yucca Flat, Nevada, USA. Year zero corresponds to 1989, when plants were originally selected.

rate of 83%, whereas no individual with an initial height  $< 25$  cm survived the 22-yr monitoring period (Fig. 3B), a statistically significant difference ( $\chi^2 = 35.03$ ,  $P < 0.0001$ ).

**Size and growth**—In 1989, the mean height ( $\pm$  SD) of the initial 53 *Y. brevifolia* was  $21.5 \pm 6.4$  cm, with a range of 12–43 cm (Table 1); 89% were 11–30 cm tall. In 2011, the mean height of the 10 survivors was  $99.8 \pm 47.1$  cm (Table 1). Mean cumulative growth of the 10 remaining plants during 1989–2011 was  $68.8 \pm 43.1$  cm, resulting in a long-term mean annual growth rate of  $3.12 \pm 1.96$  cm over 22 yr. After severe damage from herbivory, 2 of the 53 plants regrew from one or two terminal buds originating from the ground. Mean change in height between census periods was positively correlated with the amount of precipitation (hydrologic year, October–September) summed across the census period ( $n = 9$ ,  $r^2 = 0.86$ ,  $P < 0.01$ ; height [cm] =  $2.9929 + 0.0149 \times \text{precipitation [mm]}$ ).

**Vegetation associations and survival**—*Yucca brevifolia* plants were found in the bare interspaces, at the edges, and within the canopies of the perennial grass *Achnatherum speciosa* (desert needlegrass) and nine shrub species, including *Acamptopappus shockleyi* (Shockley's goldenhead), *Grayia spinosa*, *Ephedra nevadensis*, *Krascheninnikovia lanata*, *Atriplex canescens*, *Picrothamnus desertorum* (spiny sagebrush), *Lycium andersonii* (box-thorn), *Tetradymia glabrata* (horsebrush), and *Hymenoclea salsola* (cheesebush). Among these, no species had a strong relationship with *Y. brevifolia*, and ~50% of the nurse-plant relationships included co-occurrences of two or three species rather than only one. Some of the nurse plants died during the study, and new species of nurse plants also grew up around the focal plants.

The position of pre-reproductive *Y. brevifolia* in relation to perennials significantly influenced survival time ( $\chi^2 = 7.7$ ,  $P = 0.005$ ). Only 3 of the 53 *Y. brevifolia* were isolated from shrub



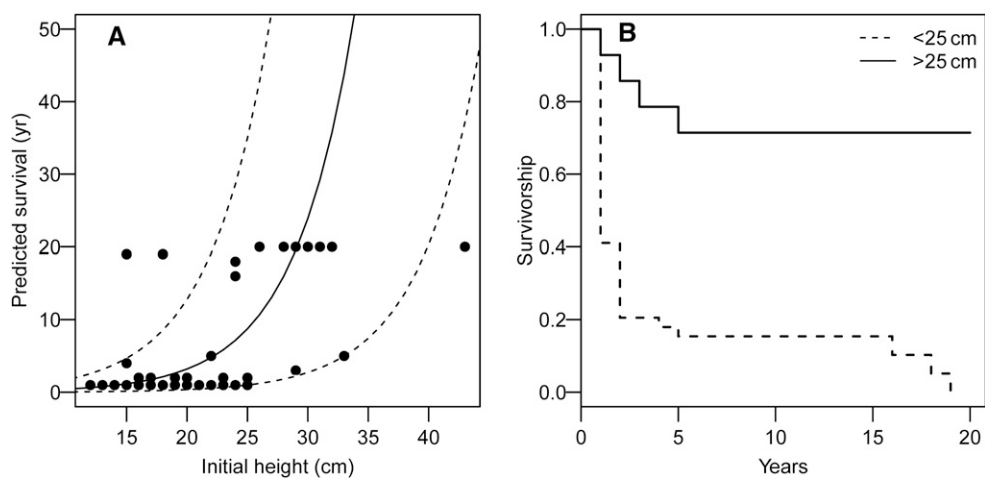


Fig. 3. The relationship between initial height of pre-reproductive *Yucca brevifolia* and survival times for 53 *Y. brevifolia* originally measured in 1989 at Yucca Flat, Nevada, USA. (A) Predicted survival times for *Y. brevifolia* derived from a regression model (Weibull distribution) with initial height of plants (dots) as predictor (note: dots overlap where multiple plants had the same initial heights). Dashed lines represent the 90% confidence interval of predicted survival times. (B) Kaplan-Meier survival curves for *Y. brevifolia* with initial (1989) heights <25 cm vs. ≥25 cm.

or perennial grass canopies, and they all were killed by *L. californicus* by March 1990. Of the remaining 50 plants, 24 were initially found at the edge of perennials and 26 were well inside the drip line of associated perennials. Survivorship curves for these two groups clearly indicate greater mortality for canopy-edge plants during the first few years of monitoring (Fig. 4). Of the 24 originally found at the edge of perennials, only 9 were still alive by August 1990 (36%), whereas 20 of the 26 found under perennials were alive in 1990 (77%). By 2009, only 3 plants (12%) remained alive that were initially found at the edge of perennials, whereas 7 that were within perennials were still alive (28%).

DISCUSSION

We found a strong relationship between the height of *Y. brevifolia* at the initial census and plant survival 22 yr later; 6 of the 7 largest individuals in 1989 survived to 2011. Our survival analyses indicate that pre-reproductive *Y. brevifolia* that are ≥25 cm tall have a greatly increased probability of survival. In

TABLE 1. Mean (± SD) height of a cohort of 53 live *Yucca brevifolia* over a period of 22 yr in Yucca Flat, Nevada National Security Site, Nevada, USA. *Yucca brevifolia* with herbivore damage could not be distinguished from the archival data; therefore, the mean increase in height included only plants with zero or positive growth values and is a subset of the number of live plants.

Year	Number of live plants	Height (cm)	Increase in height (cm)
1989	53	21.5 (6.4)	na
1990	29	22.7 (4.6)	1.6 (1.6)
1991	20	23.7 (9.6)	5.5 (9.0)
1992	19	29.7 (11.1)	4.6 (2.5)
1993	18	32.2 (11.7)	2.7 (2.0)
1994	16	30.3 (15.9)	1.4 (1.1)
2005	14	64.9 (29.4)	31.7 (18.1)
2008	12	74.8 (35.9)	10.9 (7.7)
2009	10	85.0 (40.5)	4.9 (6.8)
2011	10	99.8 (40.1)	16.0 (7.2)

the absence of natality or mortality rate estimates, Comanor and Clark (2000) assigned *Y. brevifolia* to size classes. Here, we distinguish between small pre-reproductive *Y. brevifolia* <25 cm from those ≥25 cm tall as defined by the inflection of the relationship between predicted survival and initial height. This distinction in survival between these two size classes will be useful in demographic modeling because seedlings of *Y. brevifolia* that can grow to 25 cm before the onset of drought will have the greatest probability of survival under differing climate scenarios.

Pre-reproductive *Y. brevifolia* grew between the intervals at which we measured them. Growth rates were highly variable but positive, even during years with average precipitation. Although annual growth fluctuations were considerable, growth rate averaged about 3.12 ± 1.96 cm yr<sup>-1</sup>, based on our estimates of pre-reproductive individuals. We acknowledge that our study tracked only a single cohort of pre-reproductive individuals, and tracking multiple cohorts that occur on different slopes, exposures, and elevations would provide more accurate estimates of juvenile growth rates across the distribution of this species. However, estimates of growth in our study and those of variable size classes documented in two previous studies—one in the northeast Mojave Desert (Gilliland et al., 2006) and another at three sites across the desert (Comanor and Clark, 2000)—indicate that the long-term average growth rates of *Y. brevifolia* have been somewhat consistent among size and age classes and years during the past few decades. However, more variable growth rates were reported in prior literature. Wallace and Romney (1972) reported 1.5–2.0 cm yr<sup>-1</sup>, and others reported a range of 3.5–14.3 cm yr<sup>-1</sup> (Rowlands, 1978).

Using growth rates from local estimates, the cohort of *Y. brevifolia* in our study was likely 5 to 6 yr old in 1989, with estimated emergence dates of 1983–1984. The early to mid-1980s was one of the wettest on record for most of the southwestern United States and for our site in particular (Fig. 1), providing high soil moisture during the warm July–September period required for emergence of *Y. brevifolia* (Reynolds et al., 2012). We revisited and measured the initial cohort in 10 of 22 yr, but we did not conduct systematic surveys for new emergence that may have been triggered by the high precipitation of 1983 and 1984. We

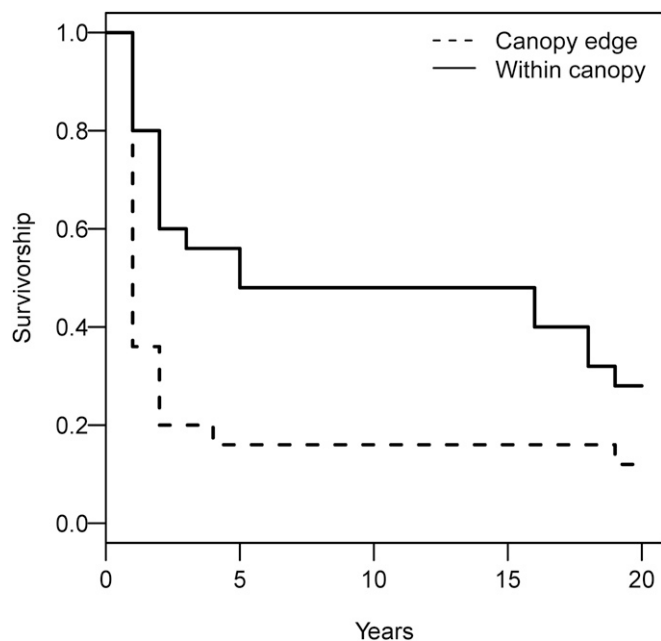


Fig. 4. Kaplan-Meier survival curves for *Yucca brevifolia* found at the edge of perennials vs. those found beneath the perennial canopies at Yucca Flat, Nevada, USA. Year zero corresponds to 1989, when plants were originally selected.

acknowledge that seedlings may have emerged in subsequent wet years (e.g., high seasonal rainfall in 1998 and 2005), but we observed only sporadic recruitment after we marked the initial cohort, precluding adequate numbers to track growth rate (e.g., 4 live plants found in 1993 and 1994 that died after 1 yr). Large emergence events have not been recorded during previous demographic studies of *Y. brevifolia*, which is consistent with the infrequent periods of high summer–fall precipitation in the 51-yr climate record for our site. Rare, pulse rainfall events such as those associated with the 1982–1983 El Niño Southern Oscillation conditions are known to be extremely important for establishment of long-lived desert plants (Cody, 2000; Schwinning et al., 2004; Miriti et al., 2007).

Although *Y. brevifolia* is known to flower when as small as 1 m tall at other sites across the Mojave Desert (specifically *Y. brevifolia brevifolia*, T. C. Esque, unpublished data), we estimate that the *Y. brevifolia* at Yucca Flat is at least 30 yr of age and still has not flowered. Considering that long-term average growth rates are 3 cm yr<sup>-1</sup> (Comanor and Clark, 2000; Gilliland et al., 2006; present study), we estimate a generation time of 50–70 yr. Furthermore, should conditions for reproduction, germination, and growth decline as a result of climate change (IPCC, 2013), generation time could be further attenuated, or the links between vital life stages could be broken, causing declines in *Y. brevifolia* in some areas. cursory examination (T. C. Esque and P. A. Medica, personal observation) of the *Y. brevifolia* population in Yucca Flat indicates that these pre-reproductive plants  $\geq 25$  cm in height represent a burgeoning population, with the potential to increase the number of reproductive individuals in coming decades.

Pre-reproductive *Y. brevifolia* plants  $< 25$  cm tall are susceptible to herbivory, particularly when consecutive years of drought reduce availability of herbaceous forage and force small herbivores to use alternative food sources, including

*Y. brevifolia* stems and leaves (DeFalco et al., 2010). In Yucca Flat, herbivory by *L. californicus* resulted in 55% mortality of pre-reproductive *Y. brevifolia*  $< 25$  cm tall in 1990. *Lepus californicus* are known to consume a wide variety of plant species, depending on seasonal availability (Vorhies and Taylor, 1933; Johnson and Anderson, 1984). Lagomorphs also have a high water requirement and need to consume vegetation that contains  $\sim 68\%$  water during the summer (Nagy et al., 1976). With scarce herbaceous plants such as grasses, shrubs, or prickly pear (*Opuntia* spp.) cactus in Yucca Flat during the 1989–1991 drought, *L. californicus* consumed numerous small *Y. brevifolia*. Drought-induced mortality for young *Y. brevifolia* ( $< 1$  m tall) was also observed at Joshua Tree National Park when a prolonged period of low rainfall followed a landscape-scale wildfire (DeFalco et al., 2010). In addition to *L. californicus*, *Thomomys* sp. (pocket gophers), *Ammospermophilus leucurus* (white-tailed antelope ground squirrels), and *Neotoma* sp. (woodrats) damaged pre-reproductive plants  $< 25$  cm tall. Following the drought, mortality due to herbivory remained low (2.5%), which is likely sustainable for vigorous populations of long-lived desert species.

*Yucca brevifolia* established in the open or near the edges of shrubs were more vulnerable to lagomorph damage than those beneath shrubs during drought. We observed increasingly greater survival among pre-reproductive plants  $< 25$  cm tall, on a gradient from no nurse plant, to those growing at the edge of nurse plants, to those growing beneath the canopies of nurse plants. The protection afforded by nurse plants is consistent with the results of another study  $\sim 150$  km south of our site in the Spring Mountains (Brittingham and Walker, 2000). Nurse plants, including *Ambrosia dumosa* (white bur-sage), *Coleogyne ramosissima* (blackbrush), *Krameria erecta* (little-leaved rhatany), and *Grayia spinosa* had more *Y. brevifolia* recruitment than expected at low and middle elevations in the Mojave Desert (Brittingham and Walker, 2000). The *Y. brevifolia* that established in the open during the 1989 census admittedly represent a very small sample ( $n = 3$ ); yet *Y. brevifolia* in the small size classes responded similarly to those in a related study (DeFalco et al., 2010). By contrast, *Y. brevifolia* of all sizes have relatively low mortality during periods of average to above-average rainfall (nearly zero in many years). Understanding resource pulse and interpulse dynamics (Schwinning et al., 2004) will be important for predicting the response of *Y. brevifolia* to climate change and other landscape-scale perturbations.

The survival rates presented here for pre-reproductive *Y. brevifolia*, along with other recent estimates of seedling survival (Reynolds et al., 2012), indicate that climatic events have a strong influence on the early life stages of this species, whether directly through drought stress or indirectly by increased herbivory during drought conditions. Several studies have modeled future distributions of *Y. brevifolia* based on projections of future climate (Dole et al., 2003; Cole et al., 2011; Smith et al., 2011; Barrows and Murphy-Mariscal, 2012). While providing insights about the future of *Y. brevifolia*, these models correlated the distribution of *Y. brevifolia* as a function of interpolated climate surfaces and did not account for the interaction between life-history stages and climate for predicting survival and distribution. By quantifying the magnitude of the direct and indirect climatic effects on early life stages, we have provided a more comprehensive means for exploring environmental stochasticity in future demographic modeling.

Understanding demographic responses of long-lived plant species to climate change may require incorporation of lag times (Svenning and Sandel, 2013). Because *Y. brevifolia* is long lived, the current distribution of reproductive adults may mask the effects of recent changes in climate on recruitment and survival of seedlings and juveniles, which are more sensitive to the vagaries of desert conditions. Recent increases in fire frequency caused by invasive species (Brooks and Matchett, 2006) throughout the range of *Y. brevifolia* have also affected all life stages of the species, and survival from intense fires is low even among large individuals (DeFalco et al., 2010). The impact of fire on seedling and juvenile survival is particularly exacerbated because fires tend to track the same heavy precipitation years that are most suitable for *Y. brevifolia* seedling emergence (Reynolds et al., 2012). Given the differential effects of climate and fire on *Y. brevifolia* of different sizes, future demographic modeling for this species will benefit from estimates of size- and age-specific survival rates. This approach will improve climate-based niche models by providing better estimates of population growth and migration rates as the species advances at its leading edge and recedes along the trailing edge (*sensu* Svenning and Sandel, 2013). Demographic models for this species must account for extended periods of increased survival punctuated by brief periods of high mortality to provide realistic population predictions for the changing regional climate.

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